ECOLOGICAL SEPARATION OF GREBES AND COOTS: INTERFERENCE COMPETITION OR MICROHABITAT SELECTION?

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Interspecific competition is assumed to be an important organizing force in natural communities and, in particular, responsible for patterns of niche diversification among ecologically similar species. However, because species' differences in resource use may not be the product of interspecific competition in sympatry, but may evolve in allopatry, "first level" (Huey 1979) evidence for competition, i.e., description of niche differences, is ambiguous with respect to defining the role of competition in producing different resource use patterns among coexisting species. This possibility tends to render even "level two" evidence for competition, e.g., the demonstration of niche complementarity (high overlap in one resource dimension associated with low overlap in another) suspect (Huey 1979). Also, the degree of resolution of patterns of resource use (i.e., the "scale" of investigation—over macrohabitats or microhabitats) can lead to different conclusions with respect to the degree to which species are ecologically separated and the factors responsible (Wiens and Rotenberry 1979, Nudds 1980).

Faaborg (1976) studied macrohabitat separation of Horned (*Podiceps auritus*) and Pied-billed (*Podilymbus podiceps*) grebes over a large area in North Dakota that included more than 500 prairie potholes. He found that below a threshold size (7.3 ha), only one species of grebe occupied the pothole. On larger potholes, as many as three grebe species (including the Eared Grebe [*Podiceps caspicus*]) were found. Faaborg (1976:397) advanced several ideas to account for these observations. These can be combined into two major hypotheses. Faaborg invoked the "compression hypothesis" to account for the disjunct pond occupancy patterns of *auritus* and *podiceps* on small potholes. Following Wedemeyer (1932), he reasoned that diet overlap must be high among prairie nesting grebes due to the absence of fish from most wetlands which are used differentially by grebe species elsewhere (Wetmore 1924, Munro 1940) and that interspecific interference competition might maintain the "fairly complete division of these species by habitat." Second, on large potholes with more than one grebe species, he hypothesized a diversity-area effect. Grebe diversity was enhanced on those potholes because of increased habitat complexity that fulfilled the niche requirements of more species.

I examined these hypotheses and the ecological separation of members

of the *auritus-podiceps-Fulica americana* (American Coot) guild, by using data on macro- and microhabitat use collected on intensively studied pot-holes in the aspen-parkland of southwestern Manitoba. The species array is ecologically meaningful because coots and grebes apparently use pot-holes similarly for nesting and foraging (Ferguson 1977). I examined wheth-er the disjunct occupancy patterns of small potholes observed at the ma-crohabitat level were the result of displacement via short-term competitive interactions or if the differential use of potholes similar at the macrohabitat level was the result of subtle differences in microhabitat use. I reasoned that if competition could account for the complementary distribution of Horned and Pied-billed grebes on similar-sized potholes (i.e., macrohab-itat), then both macrohabitat and microhabitat separation would be small. On the other hand, if complementary species' distributions and large ma-crohabitat overlap were the result of subtle differences in species' micro-habitat selection, then microhabitat separation would be large.

STUDY AREA AND METHODS

Data were collected during a study of community organization of breeding ducks from April–July 1978 (Nudds 1980). Nine potholes were selected from those on a 1.62-km² study area approximately 10 km NE of Minnedosa, Manitoba. The area was described by Dzubin (1969). Size and depth characteristics of each pothole varied (Table 1). Ponds A and I were temporary type 1 (Smith 1971), ponds B, C, E, and F were semipermanent type 3, and ponds D, G, and H were permanent type 5 potholes. All potholes held water throughout the study, but A and I were overgrown with emergent vegetation by 8 June. Pothole D was surrounded by a homogeneous cattail (*Typha latifolia*) stand, potholes C, F, G, and H by homogeneous bulrush (*Scirpus* sp.) stands, and the remaining potholes were surrounded by heterogeneous emergent vegetation associations that included those species and whitetop (*Fluminea fes-tucacea*). Ponds A and I and the edges of some larger ponds supported a diverse group of floating and submerged plants, the most common being duckweeds (*Lemma* sp.), milfoil (*Myriophyllum exalbescens*), crowfoot (*Ranunculus subrigidus*), hornwort (*Ceratophyllum de-mersum*), bladderwort (*Utricularia vulgaris*), and pondweeds (*Potamogeton* spp.). The large green alga, *Chara* sp., was abundant in ponds G and H and a smaller filamentous alga was abundant in pond E.

The perimeters of each of the nine study ponds were marked at 10-m intervals with color-coded 2-m × 2.5 × 5.0-cm wooden stakes before birds arrived in the spring. The coordinates of the grids (Fig. 1) were numbered and features of microhabitat structure were measured at each. Water depth was measured between 26 April and 1 May, and 16–23 May. Average depth for a quadrat was obtained from measurements at the four grid-points which delineated it. Three structural aspects (one vertical, two horizontal) of the vegetation and vegetation height were measured. The profile of the emergent vegetation was measured at each grid-point using a profile board modified after Nudds (1977). Quintile scores (1–5) for percent vegetation cover of the board at each of four heights (0.25, 0.5, 1.0, and 1.5 m) were esti-mated, converted to proportions of total vegetation, and substituted into $1/\Sigma p_i^2$. The mean of four values of each variable recorded determined the values for each quadrat. The pro-portions of the total area of each quadrat that were composed of dry, upland vegetation (usually grass), emergent vegetation, and open water were used as one index of horizontal

TABLE 1
SIZE AND DEPTH CHARACTERISTICS OF NINE POTHOLES AT MINNEDOSA, MANITOBA

Pond	Size (ha)	Depth (cm) $\bar{x} \pm$ SD
A	0.15	29.0 ± 3.5
B	0.87	84.8 ± 14.6
C	0.92	34.0 ± 1.7
D	0.82	78.9 ± 19.6
E	1.04	36.5 ± 19.6
F	1.71	63.8 ± 12.4
G	0.48	76.8 ± 21.3
H	0.30	101.0 ± 32.5
I	0.36	33.3 ± 7.4

microhabitat complexity. A second measure was derived by counting the number of "islands" (patchily distributed clumps) of emergent vegetation in three size categories (<0.3 m, >0.3 m but <1 m, and >1 m in diameter) in each quadrat. Island-size diversity was calculated as above. Vegetation data were collected between 16 and 23 May.

Observations on habitat use by coots and grebes were conducted from blinds entered before sunrise to minimize disturbance. Two observers rotated among the blinds to minimize the introduction of directional bias and enhance the amount of data collected. Observations were made on 62 days between 26 April and 9 July with spotting scopes and binoculars. Observers recorded the species and location of individual coots and grebes on scale maps of each pothole (Fig. 1) at 0.5-h intervals for 4 h. Values of microhabitat characteristics for the quadrat in which an individual was recorded were assigned to that individual.

I used stepwise discriminant function analysis (DFA, Nie et al. 1970) preceded by principal component analysis (PCA, Nie et al. 1970) to delineate species' differences in microhabitat use and assign relative importance to those structural habitat features that maximally segregated species. PCA was performed to reduce the amount of redundant information contained in the matrix of intercorrelated habitat variables by producing a smaller number of orthogonal principal components (PC's) which were linear combinations of the original variables. Species' scores on the PC's were used as the orthogonal discriminating variables in DFA. This step is essential if the order in which a discriminating variable is selected in a stepwise procedure is to be interpreted as its relative importance as an ecological segregator of species (Green 1979).

RESULTS

Total hours of observation (N = 372.0) were distributed among the potholes as follows: A = 28.5, B = 48.0, C = 45.5, D = 51.0, E = 46.5, F = 43.0, G = 41.5, H = 41.5, and I = 26.5. Observations on potholes A and I were terminated on 8 June when vegetation growth prevented use by birds. The number of observations of each species were *auritus*, N = 180; *podiceps*, N = 101; and *americana*, N = 856. The distribution of observations of each species varied by pond (Fig. 2).
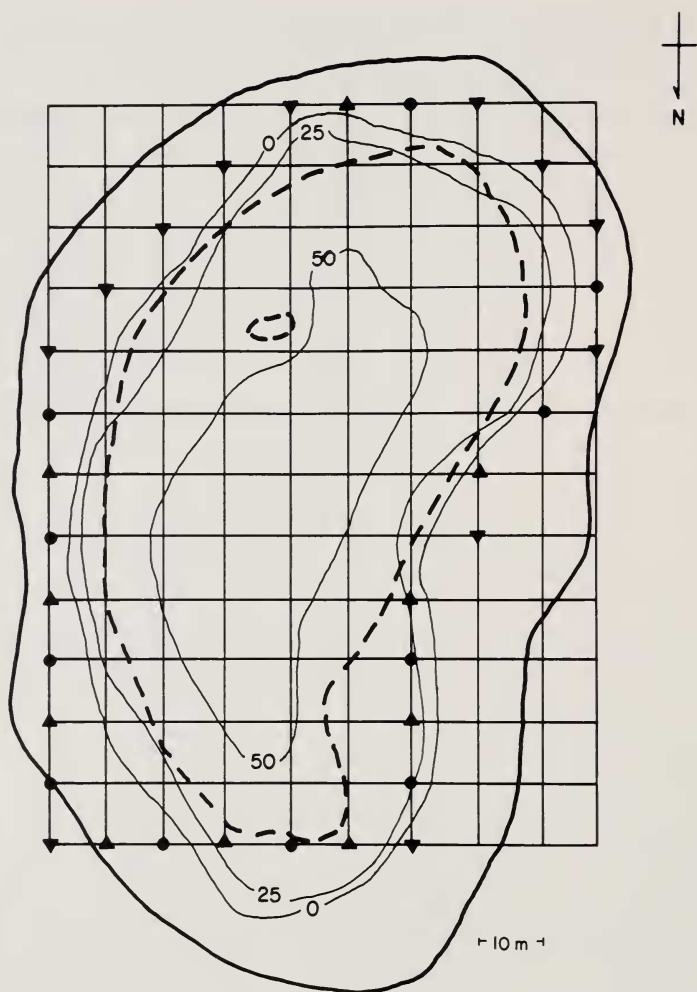
Fig. 1.   Map of pond C with stakes outlining the grid.

None of the three species used pothole I; only *americana* fed (but did not nest) on pothole A. All three species fed and/or nested on the remaining seven potholes. Birds were not individually recognizable, but it was certain (because of territorial tenacity [Ferguson 1977]) that, with the exception of potholes G and H, all potholes were occupied by more than one pair of each species.

Macrohabitat use.—There was considerable macrohabitat overlap among species (i.e., with respect to gross pothole characteristics such as size,
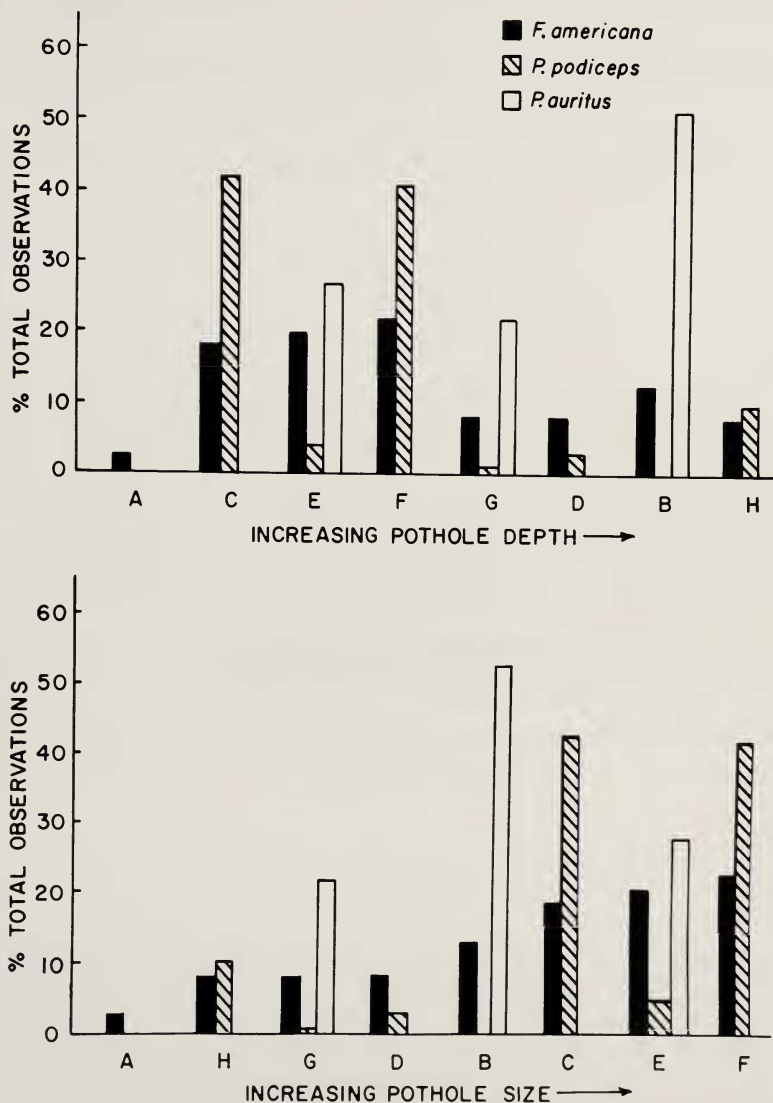
FIG. 2. Distribution of coots and grebes on pond depth and size gradients.

depth, and hence, permanence-type; Fig. 2). Coots were the most gener-
alized species with respect to pothole use. Pied-billed Grebes tended to
use shallow potholes surrounded by homogeneous stands of *Scirpus* (C
and F); Horned Grebes used deeper potholes (G and B, but also E) with
(G) or without (B and E) homogeneous stands of *Scirpus*. Pothole size was
also an inadequate species' segregator (Fig. 2).

TABLE 2

MICROHABITAT FEATURES AND PRINCIPAL COMPONENT LOADINGS FOR THE GREBE-COOT GUILD AT MINNEDOSA, MANITOBA

Variable	Description	PC 1	PC 2
Depth	water depth	−0.75	
L1		0.91	
L2	vegetation density in each	0.94	
L3	of four layers	0.80	
L4	(see text)	—	
SUML	ΣL	0.94	
DIVERVEG	vertical complexity of vegetation (see text)	0.95	
VEGHGHT	vegetation height	0.88	
UPLAND	proportion of quadrat that	—	
EMERG	was upland or emergent	—	
WATER	vegetation or water	0.75	
DISPAVEG	spatial complexity of vegetation (see text)	0.87	
NA	number of 'islands' in each		—
NB	of three size categories (see		0.66
NC	text)		0.60
SUMN	number of 'islands'		0.73
DICLUMPS	'island-size' diversity		0.73
Cumulative % variance explained		70.4	

Two grebe species occurred on two of the seven potholes, even though all of the potholes were smaller than the 7.3-ha one-species threshold level identified by Faaborg (1976). Nevertheless, the almost complete complementarity of *auritus* and *podiceps* distributions is as Faaborg (1976) observed. Is this the result of competitive exclusion, or between-pond differences in microhabitats used by each species?

Microhabitat use.—Two independent microhabitat dimensions (Table 2) were identified by PCA and together accounted for >70% of the total variance among the original microhabitat variables. PC 1 described a continuum of microhabitat structure from deep, open water sites with no emergent vegetation to tall, dense, spatially uniform stands of emergent vegetation in shallow water. PC 2 was a gradient of spatial microhabitat complexity (vegetation interspersion, Table 2).
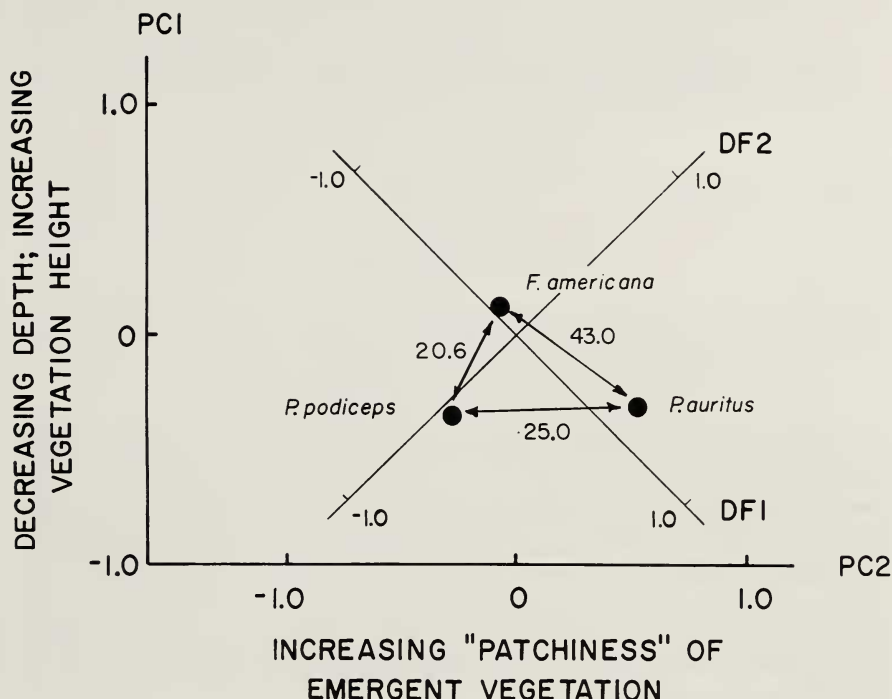
FIG. 3. Relation of coots and grebes in 2-dimensional microhabitat space and the discriminant axes along which the species are maximally segregated.

Coots occupied microhabitats with shallow water; grebes used deeper portions of ponds (Fig. 3). Pied-billed Grebes occurred in the densest emergent vegetation, *americana* was intermediate in that respect, and *auritus* used microhabitats with the greatest degree of water-vegetation interspersion (Fig. 3).

DFA identified PC 2 as the best ecological segregator of species. Microhabitat separation was large ($F = 34.53$, $P < 0.0001$), but species' pairwise niche separation varied from little separation between *americana* and *podiceps* to large separation between *americana* and *auritus* (Table 3). The two grebe species were highly separated in the vegetation interspersion dimension (Table 3). After entry of PC 1 in the discriminant model, overall species separation decreased but still differed markedly ($F = 31.24$, $P < 0.0001$). There was a greater degree of species' overlap in the depth dimension than in the spatial complexity dimension, which caused overall species' separation, and the pairwise separation of *amer-*

TABLE 3

MICROHABITAT SEPARATION[a] MATRICES IN ONE- (UPPER) AND TWO-DIMENSIONAL
(LOWER) DISCRIMINANT SPACE FOR THE GREBE-COOT GUILD AT
MINNEDOSA, MANITOBA

	F. americana	P. podiceps
P. podiceps	4.68	—
P. auritus	58.63	47.35
P. podiceps	20.58	—
P. auritus	43.02	25.03

[a] Maximum among-to-within species variance in microhabitat use.

icana-auritus and *podiceps-auritus* to decrease. However, the pairwise separation of *americana* and *podiceps* increased (Table 3). Thus, for the species-pair (*americana-podiceps*) occupying the most similar microhabitats with respect to vegetation interspersion, separation on the depth gradient was greatest. For the species pairs (*americana-auritus* and *podiceps-auritus*) that were largely separated on the gradient of vegetation interspersion, separation on the depth gradient was less. These results suggest complementarity of species' distributions along uncorrelated gradients of microhabitat structure.

DISCUSSION

There was considerable overlap in habitat use as measured by gross pothole characteristics such as size, depth, and permanance, but grebe species had largely complementary distributions over those macrohabitat gradients. Coots were generalists and used all types of wetlands (Sugden 1979). Grebe distributions can be explained without invoking competitive displacement via interspecific aggression. Grebe species used structurally different microhabitats; those microhabitats were differentially represented on potholes otherwise similar with respect to macrohabitat features.

Species' separation was greatest along a microhabitat structure gradient reflecting "patchiness" of emergent vegetation. *P. auritus* selected microhabitats with greater vegetation interspersion (Sugden 1977) an important aspect of nest placement by that species (Ferguson 1977). Conversely, *podiceps* selected microhabitats with dense emergent vegetation (Faaborg 1976, Glover 1953). Chabreck (1963), however, reported that breeding *podiceps* in Louisiana used microhabitats similar to those used by *auritus* in the prairies. The breeding range of *auritus* does not extend to Louisiana (Ferguson 1977) and the use of structural microhabitats there by *podiceps* may be an example of ecological release of *podiceps* into microhabitats

ordinarily used by *auritus*. That hypothesis assumes that exploitation competition in evolutionary time contributed to evolved species' differences in microhabitat use. Nevertheless, it is unnecessary to postulate that short-term interference competition between *auritus* and *podiceps* is responsible for their disjunct use of small ponds in the prairies.

Schoener (1975:248) postulated a continuum of mechanisms responsible for differential habitat use from behavioral (short-term) interference and displacement to genetic (innate habitat preferences). Grebes are divergent in habitat use (i.e., nearer the 'genetic' end of Schoener's continuum) and species' coexistence is enhanced by habitat complexity which fulfills the requirements of each species (Faaborg 1976). In this context, the significance of interspecific aggression as evidence that species compete for space is diminished and viewed as simple defense of, say, nesting platforms, which are attractive to conspecifics and other grebes, coots, and ducks as loafing sites (Ferguson 1977). Morris (1981) hypothesized that among organisms that are habitat selectors, most encounters will be with conspecifics, and occasional interspecific aggressive encounters may result because individuals behave to all other individuals as if they were conspecifics.

Lack of evidence of competition in the short-term does not mean that competition was unimportant in shaping observed species' differences in resource use. Competition may be periodically enhanced by depressed resource levels, particularly in variable environments like the prairies (Wiens 1977). It would be informative to follow the dynamics of species' habitat use over time for the grebe-coot guild through periods of resource depression and super-abundance.

SUMMARY

Faaborg (1976) studied macrohabitat separation of grebes on prairie potholes and postulated (1) that grebe diversity was related to an area-diversity effect on potholes greater than 7.3 ha, and (2) that the occurrence of single grebe species on potholes less than 7.3 ha was related to interspecific interference competition. A study of macro- and microhabitat use by coots and grebes revealed large overlap in macrohabitat use but significant differences in microhabitat use. Only one grebe species occupied small potholes because potholes differed with respect to the amount of vegetation-water interspersion used by each species; this results in disjunct species distributions. Presence of suitable microhabitat thus determines grebe diversity over all sizes of potholes, and it is unnecessary to postulate that short-term interference competition is responsible for single species occupancy of small potholes.

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